The Origin and Development of Bulbs in the Genus Erythronium

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FREDERICK H. BLODGETT

A DISSERTATION

SUBMITTED TO THE BOARD OF UNIVERSITY STUDIES OF THE JOHNS HOPKINS UNIVERSITY IN CONFORMITY WITH THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

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THE ORIGIN AND DEVELOPMENT OF BULBS IN THE GENUS ERYTHRONIUM[1]

FREDERICK H. BLODGETT

(WITH PLATES VIII–X AND SEVEN FIGURES)

Introduction

The genus *Erythronium* includes some fifteen species of bulbous plants of the north temperate zone, one of which occurs from the Pyrenees, across France, southern Europe, and Asia, to Korea and Japan. The remaining species are North American.

The plants are perennial through the annually renewed bulbs. These are developed at gradually increasing depths from the seedling to the flowering stage, after which they are formed at a nearly constant depth in the soil. The bulb consists of a few thick scales surrounding the stem apex; the aerial structures push upward from the base through the cavity inclosed by the inner scale. The first aerial structures are single leaves, two leaves and flowers appearing only after several years.

Special details of the development of one or another of the species have been examined by several writers; but some stages have been omitted in these accounts, and in others some obscurity exists as to the exact nature of the structures mentioned. A consecutive account of the development of the plant, with special reference to the origin and structure of the stem apex, and its outgrowths, from its inception in the embryo to the final formation of the flower bud, is the subject of this paper; which is thus a study of the vegetative development of the sporophyte, consideration of the gametophyte being omitted.

Erythronium americanum is taken as the basis of the study, since material of this species is abundant in the vicinity of Baltimore, and especially since it shows more specialization in its vegetative development than do the other forms. Comparisons have been made with other species, as will be noted, and the

[1] Contribution from the Botanical Laboratory of the Johns Hopkins University, no. 14.

differences found have a probable bearing upon the evolution of the genus.

Material was killed in chromacetic acid, and cut usually 10 μ in thickness; except in the case of the hard seeds, no special methods were necessary.

To Professor DUNCAN S. JOHNSON the author wishes to express his thanks for helpful criticism and maintained interest during the progress of the work.

Germination

The flowers of *Erythronium americanum* appear during the first week of April in this region, and the seeds ripen early in June, from which seedlings arise the following March. The main body of the seed measures about 4×2 mm., but a spongy spur at the chalaza and a fleshy raphe nearly double the bulk of the seed, subject to individual variation. The embryo in the ripe seed is slightly pointed toward the micropyle, but is otherwise undifferentiated (fig. 1).

Germination begins about the middle of September, when the seed becomes moistened by the fall rains, and the embryo begins to elongate. The growing embryo enlarges first to occupy the space filled by the spongy endosperm, in which it is imbedded, ordinarily by the first week of October. The tip of the cotyledon is organized into a haustorial organ, by which the hard endosperm is absorbed. Elongation proceeds slowly during the fall, so that the embryo is half the length of the seed in December (fig. 2). The rate of growth seems to be closely related to the abundance of moisture in the soil. The tip of the radicle is pushed about the end of the year through the micropyle. The stem apex at this stage appears in a narrow cavity extending from the surface nearly to the center of the tissue just behind the radicle. The hypocotyl does not elongate, and is practically absent. As the embryo continues to elongate, the stem apex is carried forward, and retains a constant position in relation to the radicle during the elongation of the cotyledon (fig. 3). The zone of elongation during this time is in the lower part of the cotyledon, just above the cavity in which the stem apex is situated. Growth is nearly vertical, and after penetrating the soil 1–3 cm. the descending axis comes to rest.

When the endosperm has been exhausted, the elongation of the descending axis ceases. The zone of elongation in the cotyledon is now located near the upper end of the cotyledon, so that the tip of the cotyledon is withdrawn from the empty testa, and elevated into the light, much as in *Allium* (SACHS 18). From the haustorial cells at the tip of the cotyledon two vascular bundles extend downward to the base of the root, just below the level of the stem apex, as in *Tulipa* (IRMISCH 11). In some species (*E. grandiflorum*, and *E. Hartwegii*) there are three cotyledonary bundles (SARGANT 19). After reaching the light, the cotyledon attains a total length of 8–10 cm. above the soil line (text fig. 6), and the elbow formed in the withdrawal from the seed coats gradually straightens. The cotyledon is cylindrical below, but may be considerably flattened in the upper portions, the two bundles lying side by side (figs. 4, 5).

The apical dome becomes differentiated during the descent of the stem apex, and the cavity in which it is inclosed changes into a curved pocket by the elongation of the walls of the cavity (figs. 6–10). The apex then rises as a dome from the bottom of the pocket. The space about the apex has a depth about equal to its width when the descending axis comes to rest. The thickness of the walls decreases from the axial to the opposite side, which lies immediately below the opening from the interior of the cavity to the exterior. The base of the cotyledon thus comes to form a sheath about the stem apex. The radicle has as yet grown but little; soon, however, the primary root is organized and advances from the end of the descending axis (text fig. 1). The primary root is the only one in the life cycle which responds positively to gravitation. At the base of the root a considerable cushion is formed, upon which root hairs are produced abundantly. By the growth of adjacent tissues the base of the root becomes oblique, and seems to be fused to the side of the cotyledonary sheath for a short distance (figs. 6–9). The stem apex, or plumule, has so far no vascular supply from the rest of the seedling, the cells below the apical dome being meristematic and undifferentiated as yet into tissues. The plumular trace is inserted upon each of the two cotyledonary bundles, just before they unite to form the root

stele, the region of fusion being about 0.5 mm. in length (figs. 16–20). This theoretically constitutes the "hypocotyl" in these seedlings (SARGANT 19).

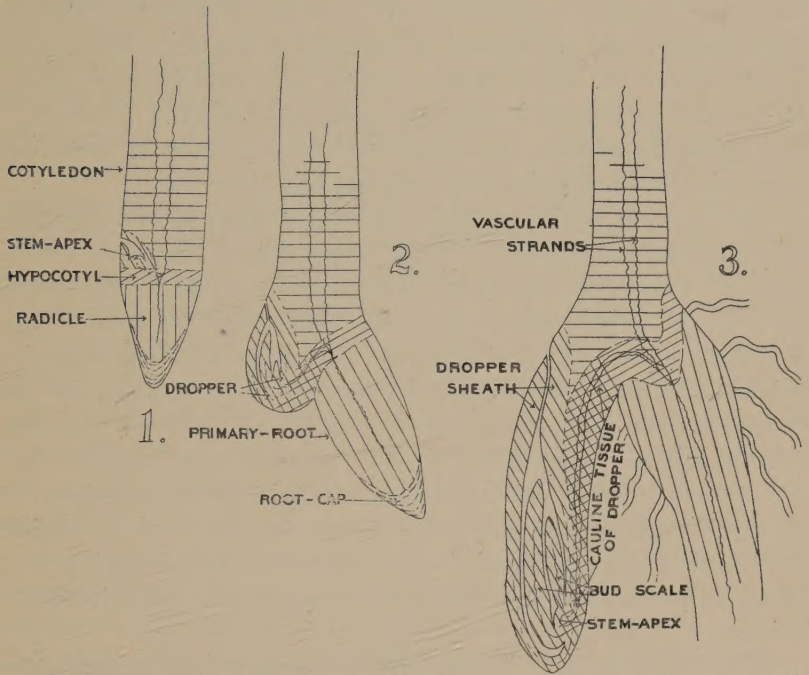

FIG. 1.—Diagram showing development of seedlings: *1*, descending axis during first stage; *2*, inception of droppers and development of root; *3*, dropper actively elongating downward, second stage of descent.

First vegetative period

The cotyledon functions as the first foliage leaf, and provides material for the further descent of the stem apex. Abundant stomata and large intercellular spaces are present in the body of the cotyledon; moreover it has the power of recovery from wilting to a high degree. This was found by allowing the soil to become dry and then watering, when seedlings which had become prostrate recovered their erect position, unless the cells had actually been killed. The cells nearest the tip were the first to show the effects of too great drying.

Soon after the cotyledon becomes active photosynthetically,

and the primary root is protruded into the soil from the end of the descending axis, the further descent of the stem apex begins. The sheath in the base of the cotyledon, in which the apical dome is located, elongates by the proliferation of the cells in the walls of the sheath so that the base of the cavity is lowered in reference to other points. As the structure so formed is positively geotropic in its growth response, it may conveniently be called a "dropper." The apical dome, being inserted at the base of the sheath, is carried forward in the elongation as a terminal bud (figs. 10, 13).

The dropper originates from the cotyledonary sheath through the irregular distribution of the dividing cells in the walls of the sheath. The base of the sheath is displaced laterally by the multiplication of cells between the apical dome and the axis of the cotyledon (figs. 6–8). This pushes the base outward from its original position. While the displacement is proceeding in the lateral direction, an elongation is also taking place, so that the dropper begins to push forward into the soil during its displacement. Soon after the axis of the dropper becomes established as a direction of growth, the zone of elongation becomes confined to the region immediately adjacent to the base of the apical dome. This places the growing tissue close to the apex of the dropper, as if it were a rhizome.

The inclosing walls of the dropper do not grow equally, the axial wall elongating more slowly at first than the abaxial, resulting in a lagging behind of the apical dome, in reference to the base of the sheath cavity. The stem apex thus becomes located on the side wall, instead of at the base of the sheath (fig. 13). The axis of the dome itself may become almost horizontal through this displacement. The oblique position of parts inaugurated at this stage of development persists through the life cycle, including the deep-seated bulbs of the flowering individuals. The lateral location of the stem apex at the base of the sheath cavity causes a distortion of the outgrowths from the apical dome as they appear. The apical outgrowths push upward into the cavity about the stem apex, and thereby appear to be at nearly right angles to the axis of the dome (fig. 13). The rate of growth of the apical dome and that of the developing scale is so nearly identical that the dome

itself is lost as a distinct group of cells. When the scale has so far developed that the margins of the leaf rudiment meet in front of the median line of the scale, then the apical dome becomes distinguishable again. The dome then forms a low mass of cells projecting from the face of the axial side of the scale into the space inclosed by the united margins. Continued growth soon makes the dome more conspicuous, and at the same time readjusts its position to a more central point (figs. 10, 12, 13). The tissues of the scale rudiment and of the stem apex are nearly alike in their staining qualities, and continue to be meristematic until a considerable size is reached. Thus in the first stages of scale formation, the growth in length of the apical dome and the growth in thickness of the scale rudiment are so nearly equal that there is no difference in staining reaction to aid in separating the two morphologically different tissues. It is not until the scale leaf has inclosed the apical dome by the forward growth of the margins of the scale, that the dome is to be separately recognized. This obscuring of the apical dome appears to be a recurring feature in the normal development of the bulbs, as the successive bulb scales are formed.

The dropper grows downward to a distance varying from a few millimeters to 4 (rarely 5) cm.; in most cases the dropper is about 2.5 cm. in length. This growth is accomplished during the period of activity of the cotyledon as a leaf, by which the needed starch and other materials are elaborated. At the end of three or four weeks of development, the apical bud within the dropper sheath becomes enlarged by the deposit of storage starch, and the stem apex with its inclosing bulb scale becomes the primary bulb (fig. 14). The seedling dies from the apex of the cotyledon backward, gradually involving all tissues except the bulb, which thus becomes isolated in the soil. The withered walls of the dropper sheath form a husk about the bulb. In the axil of the dropper sheath a bud is formed, which rarely develops.

During the active descent of the dropper, vascular connection from the stem apex to the base of the cotyledon is maintained through the bundles in the axial wall of the dropper. This tissue is to be regarded as cauline in character, since it terminates in the growing point of the stem. In its earliest stages the vascular

strand appears as a few elongated cells between the base of the apical dome and the base of the cotyledonary bundles (figs. 8–10, 16–20); as the dropper elongates these cells increase in number by additions at the growing end, and become more completely differentiated into vascular elements (figs. 8, 11, 13). At the end of the strand branches are given off into the scales developed from the apex. The vascular elements are only slightly developed in the bulb bundles, since there is little strength required, and the bundles are surrounded by abundant parenchyma. The spiral vessels are the most easily distinguished parts of the bundles.

During the summer the bulb shows no external signs of activity, but the stem apex is then organizing the first foliage leaf for the second vegetative season. In its inception the leaf resembles a scale leaf, but soon becomes differentiated into a blade and a basal portion. By the elongation of the base, the blade is elevated above the stem apex (fig. 15, *l*). The apical dome is thus left in a position simulating that of an axillary bud, with the leaf as its subtending organ. But the further development of the dome, as well as its immediately preceding history, identifies this as the stem apex. The leaf and the apical dome are in the relative development given about July 1.

In the development of the foliage leaf, the elongation of the petiole lifts the lamina above the stem apex before the latter becomes inclosed by the development of the margins of the blade. The margins grow outward from the median portion of the leaf rudiment, their edges passing each other above the level of the stem apex. The base of the petiole grows about the stem apex, so that this becomes inclosed in a sheath much as was the apical dome in the cotyledonary sheath. A small opening connects the cavity of the sheath with the space outside the petiole in the bulb.

At this time there appears in the axil of the leaf an axillary bud, which from its position in reference to the apical dome seems to be borne upon the surface of the dome, rather than to be truly axillary to the leaf. A bud is also developed in the axil of the inclosing scale. The stem apex develops usually two bulb scales during the late summer, thus forming a bulb rudiment at the base of the leaf by the close of the year. In these primary bulbs the stem

apex alone develops into a bulb in most cases; but in older plants the axillary buds may also develop into bulbs. When the bulbs of any age are renewed *in situ*, the apical bud forms the single new bulb; but when there are runners developed, the axillary buds also form bulbs, being then the terminal buds of runners which become isolated in the soil as in the case of the primary bulb from the dropper.

Second vegetative period

The second vegetative period in the life cycle of the individual begins in September, when the roots protrude from the base of the primary bulb. These are few in number, three in most cases, and do not respond positively to gravitation. The root rudiments originate just below the region where the vascular strands from the dropper give off branches into the stem apex and the bulb scales. These stages are shown at *r* in figs. 24, 26, 27. The roots grow nearly straight from the point of origin to their limit of growth. They maintain a spatial relation toward each other so as to be equidistant in the soil. The oblique position of the base of the bulb makes the cluster of roots which radiate from the base appear lateral (JOST **14**, p. 27) at the lower end of the bulb. In the older bulbs the roots are more numerous, and their lateral insertion is but slightly changed. The position of the roots in the soil is such as to define a nearly flat cone, with its axis in line with the axis of the apical dome. The angle taken by the axis of the cone varies slightly as the obliquity of the individual bulb differs, but lies close to 45° to the vertical. Under experimental tests, different positions of the bulbs used did not change the position of the axis of the cone of roots in reference to the axis of the apical dome, although the latter was itself placed in abnormal positions in respect to the vertical. Roots are rarely found within the conical mass of soil outlined by most of the roots; when so found, the roots are very numerous and some are crowded away from the peripheral portion of the meristem cells in the base of the bulb.

During their growth from the point of their inception to the surface of the bulb, the root rudiments pass through the tissues at the base of the bulb, a thickness of 1–3 mm. according to the size of the bulb. In passing through the bulb the advancing tip of

the root rudiment appears to come into contact with the cell walls at intervals only. This is indicated in sections by the presence of a cavity about the root tip, the bulb parenchyma being separated from the root itself by a space in which there appear no cell walls. In the cells at a little distance from the line of advance of the root, scattered starch grains appear, and the normal starch content remains in the bulb parenchyma farther from the root cluster (text fig. 2). It appears that the starch is first removed from the cells in the path of the advancing root rudiments, then as the root is organized and grows forward, the cells themselves are disintegrated, leaving a clear pocket immediately about the conical end of the root. Only at the sides of these cavities were there any flattened cells, as if contact had occurred between the root tissue and the surrounding parenchyma. But as the root issues from the base into the soil, there is a collar of cells about the base, which constricts the root at this point to a slight degree.

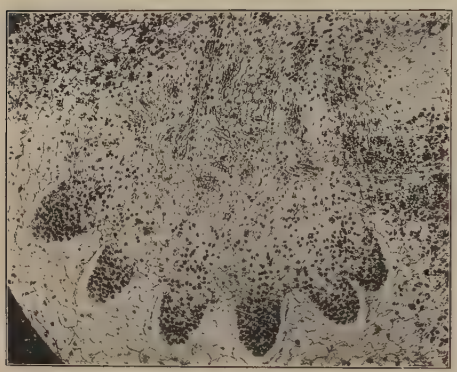

FIG. 2.—Base of bulb, showing inception of roots in summer; ×25.

The number of roots increases with the age of the bulb, in large flowering individuals reaching 30 or 40. These all die at the close of the season, and a new set is formed for the next year, even if the new bulb is developed *in situ*. The roots have no contractile cells, and act only as absorbing organs; the shape of the bulb helps to anchor the plant in place. Root hairs are produced in abundance in a moist chamber, or in nature on those parts of a root which may pass through an air space in the soil. Where the soil is in close contact with the root, the root hairs are inconspicuous or undeveloped (in this connection see **8**, p. 146). The meristem tissue from which the roots arise continues to form new root rudiments for some time after the main supply of roots is formed. Thus a new crop of roots may be formed after the already developed

one has been cut off; or if in handling the bulbs the roots present become dry, new roots are protruded among the bases of the old. In sections young rudiments are to be found in the basal tissue until nearly the close of the growing season.

The roots have a well-developed endodermis, formed of two, or rarely three, cell layers just outside the usually triarch stele (figs. 21, 22). The endodermis is delicate in the seedling, but well developed in the older roots.

The stem apex becomes more active after the roots are established in the soil, and develops the bulb rudiment from the apical bud. There are two axillary buds; one of these is in the axil of the first leaf (cotyledon), the base of which elongated to form the dropper, and on the death of the seedling dried out to form the husk. The other bud is axillary to the inner scale, which forms the bulk of the bulb as it lies in the soil until the second growing season begins. In the primary bulbs neither of these buds ordinarily develops further; but in older plants these, as well as the apical bud, form runners. During the mild periods of the winter and early spring the leaf is protruded from the bulb, and appears above the soil about the middle of March. The first leaves are about 1 cm. in width by 3–5 cm. in length, a little more tapering than the older leaves, but in other respects like them. They last for six to eight weeks, and then disappear by retrogressive withering. During their activity the bulb rudiment at the base of the petiole enlarges to its full size as the secondary bulb.

The starch stored in the primary bulb is used in part in the formation of the aerial structure (foliage leaf), in part also in the building of the new bulb. The bulb gradually disappears as the new bulb develops, the older tissues becoming free from starch and reacting to the Fehling test for sugar as the season advances and the new bulb enlarges. When the leaf begins to wither, in late May, there is practically nothing left of the primary bulb except its husk; this still incloses the base of the petiole, which forms the husk of the secondary bulb. After the death of the foliage leaf, the bulb is dormant until the roots are developed in September, as the first step in the third vegetative season. But in the interval the stem apex organizes the foliage leaf, and organizes the buds

in the axils of the two bulb scales as runner rudiments, in preparation for the next year. The details are similar to the same steps in the primary bulb.

Immature stages

Between the development of the secondary bulb and that of the bulb which bears a flowering shoot, an indefinite number of years may elapse. The least number of intervening seasons has been calculated to be three, making, with the first and second seasons, a minimum of five years from seed to seed. Many individuals at any stage fail to produce runners in any one season, and their immature period is correspondingly lengthened. Others fail to gain any depth in the development of the new bulbs from runners, and these also lengthen the interval between the first and final bulbs. With the production of the flower the activity of the primary stem apex ceases, the subsequent bulbs being developed annually each from a bud at the base of the aerial shoot. In the immature individuals more than one bulb is formed in average seasons in four species,[2] more or less specialized structures being developed for this purpose. Most of the plants producing runners in *E. americanum* in any one season after the second bulb have three at a time. One of these is the apical bud, the other two are axillary buds. The relation of these three buds is shown in figs. 28–33; these buds have been mentioned in a preceding paragraph as related to the development of the runners. The runners in the four species mentioned are not uniform in character, since in the development of the elongated structure of the runner different tissues are made use of by the plant in different species. *Erythronium americanum* is the most specialized in its development, but it is the clearest morphologically.

Each of the runners in *E. americanum* comes from a bud within the bulb (text fig. 3), the buds being made up finally of two scale leaves and a stem apex inclosed by them. The buds are inserted upon the tissues of the bulb in such a manner that the outer surface

[2] These are *E. americanum*, *E. albidum*, *E. propullans*, and *E. Hartwegii;* others rarely multiply. In *E. propullans* the adult plants have a lateral runner in addition to the renewal bulb within the old. Under cultivation axillary buds in adult bulbs in most species develop into bulbs.

of the external scale is united to the subtending portion of the bulb. As the buds begin their development, the first growth is eccentric and pushes the base of the bud outward from its first position, leaving the bottom of the bud free from contact with other tissues. Subsequent growth on the part of the bud is chiefly located in a zone about the base of the scale, close to the insertion of the inner scale upon the base of the bud. As the point at which the bud is united to the bulb tissue is above the zone of growth, the growing zone tends to push the base of the bud away from its original position and downward into the soil, as was the case in the beginning of the dropper. This elongation is confined almost entirely to the outer scale, the inner scale and the inclosed stem

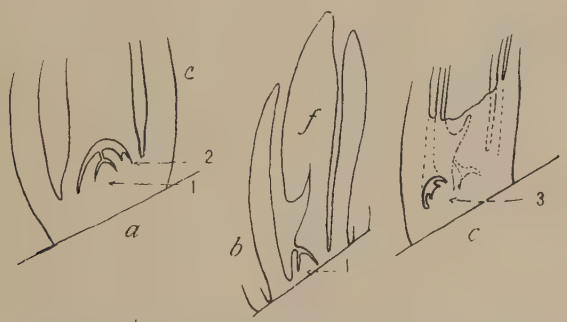

FIG. 3.—Space relations of buds in immature bulb of *E. americanum:* *1*, stem apex; *2*, inner axillary bud; *3*, outer axillary bud; ×10.

apex being carried along passively, as the terminal bud in the runner (cf. fig. 13). The runner is thus formed by the elongation of the outer scale of the bulb rudiment, and in the case of the apical bud and the inner axillary one, they burst through the inclosing base of the petiole when the base of the bulb has been penetrated. In these runners the scale is definitely organized in the bud, before any elongation begins, and the base of the foliage leaf takes no share in the formation of the runner, as did the base of the cotyledon in the seedling dropper. In other species[3] the sheathing base of the foliage leaf contributes to the developing runner, as in the case of the cotyledon and dropper. The elongation in this type of runner is the same as that in *Tulipa* (ROBERT-

[3] *E. albidum* for example.

SON 17, IRMISCH 10), in that the protrusion of the petiole base carries with it the bud inclosed by the petiole sheath.

In *E. albidum* two runners are usual, while the species from the western United States and Eurasia normally form but one. The length of the runner may be so much reduced as to pass unnoticed, but unusual conditions may demonstrate the presence of the typical structures not otherwise distinct. When but one runner is formed, or when the bulb is renewed *in situ*, the main stem apex is the active structure, the axillary buds if present remaining undeveloped.

There seems to be a moisture relation on the part of the growing runners. Plants of *E. americanum* growing in well-drained wood soil were found in several cases to have few runners; while other plants of similar general appearance, but in wet soil at the bottom of the same hill, showed runners in most individuals. It is noticeable about Baltimore that those individuals which grow in heavy, wet soils produce runners earlier and more abundantly than those of drier habitats. The development of abundant runners would hasten the attainment of full depth on the part of a particular group of plants, and this would be manifest in the greater frequency of flowering plants in a colony of stated size. The conditions under which the plants grow are evidently directly related to flower production, as the abundance of bloom has been observed to be associated with abundance of moisture in each of the habitats examined during the work here discussed.

In moist chamber experiments it was found that the tips of the runners were positively geotropic when lying on the top of saturated sphagnum, a little free water being present in the dish (fig. 23). In the absence of free water in the dish, the response was less marked, and in mere dampness it was a negligible quantity. In testing to determine whether the downward growth of the tips under abundant moisture is due to a moisture response or to gravitation, experiments were made with moist sphagnum in different positions in reference to the growing runners. The slow growth and the sluggish response on the part of the runners made the experiments inconclusive. In the moist chamber a period of two or three weeks was needed to carry through a set of tests.

The slow growth of the runners made experiments with them unsatisfactory when using the centrifuge or klinostat, but the evidence obtained tends to confirm the indifference to gravitation noted under natural conditions.

The lateral displacement of axillary buds, with little subsequent elongation, occurs in species of *Gagea* (Irmisch 10). In *G. minima*, *G. lutea*, and *G. pratensis* there are short protrusions of the bulb rudiment as if about to form a runner, but the elongation is not sufficient to burst through the base of the bulb. The sheath in which the new bulb is formed is the base of one of the leaves, which forms a pouch or pocket about the enlarging bulb rudiment. In *Tulipa* the base of the petiole not only forms the pocket immediately about the bulb rudiment, but elongates in such a manner as to carry the inclosed bud forward into the soil as the terminal bud in a hollow runner. This is the type mentioned above as occurring in *Erythronium albidum* and others in respect to the apical bud. In each of these cases the bud tends to become deeper than its predecessor, but in *Allium vineale* and *A. Scorodophrasum* (Irmisch 10) the buds are borne upon independent bases, which elongate during the growth of the buds, so that the the buds are elevated from the first position and thrust out of the top of the bulb. In the cases first mentioned the buds are attached laterally to the bulb tissue from which they arise, and are thus unable to rise above their insertion, but must descend more or less sharply in the individual species.

Structure of runners

The structure of the runner may be understood from the accompanying diagram (text fig. 4). Such a bud as that of *Allium vineale*, which elongates in the region below the insertion of the bud scales, would be elevated above its original position; this is the normal erect bud. On horizontal rhizomes a bud assumes the position shown in *2* of the diagram at the close of the period of elongation. If this position were taken during active progress through the soil, a great amount of resistance would have to be overcome in pushing the erect bud forward. This exact arrangement of parts has not been noticed in nature; but it occurs slightly modified in *Erythronium propullans*. In this species the

lateral runner issues from the side of the shoot with the bud at the tip in an erect position. But the bud does not stand freely exposed above the general surface of the runner stalk. The region immediately behind the bud, where the scale and cauline tissue are fused, thickens vertically, so that the bud receives the support of the adjacent tissue for its whole height, and is therefore not subject to transverse strain tending to invert it upon its base.

In the absence of supporting tissue for the height of the bud, the elongating runner would tend to advance the base of the bud

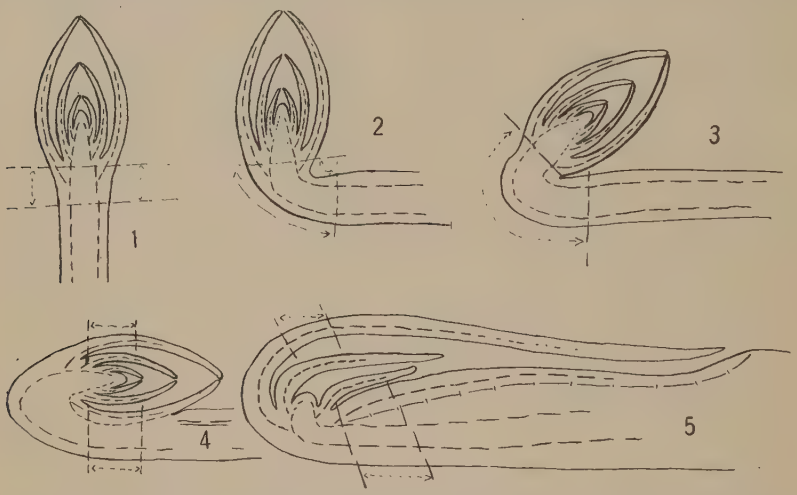

FIG. 4.—Evolution of *Erythronium* type of runner: *1*, normal bud, terminating stem (*Allium*); *2–4*, hypothetical stages, with horizontal stem; *5*, anatropous bud of *Erythronium* runners; dotted lines and arrows indicate zone of elongation in each case.

beyond the rest of the bud, as in no. *3*, since the unsupported parts of the bud would be retarded by friction in passing through the soil. The tendency under such conditions would be for the adjacent surfaces of the bud scale and the stalk to fuse, as suggested in no. *4*. Up to this point the scales of the bud have taken no part in the elongation of the runner or of the bud at the tip; but with the fusion of the bud with the surface of the runner stalk, either the zone of elongation must shift to a point outside the fusion region, or the scales must be included in the growing zone; otherwise the tissues would be under continued but irregular strains. In the

runners of *E. americanum* the structure sketched in no. 5 is present. The zone of elongation is close to the organic base of the bud, while the bud scale is fused for its full height with the stalk of the runner. There are no disruptive strains in this case, for the external scale of the bud elongates as fast as does the cauline tissue of the runner; that is, the scale leaf, like a foliage leaf of the same plant (ROBERTSON 17), elongates in the basal zone; the stem elongates in its apical region, and as the two are folded back upon each other, the two growth regions are continuous about the inclosed bud. The position of this region of elongation is indicated by the space between the diagonal dotted lines in no. 5.

The cauline tissue in the runner is represented by the vascular bundles which unite the terminal bud in the runner tip to the base of the parent bulb. The presence of foliar tissue on the same side of the runner is indicated by the course of the vascular bundles, which turn backward at the base of the scale, and supply the inner face of the axial wall of the dropper in the same manner as the thin abaxial wall, where there is no tissue other than the scale. (Cf. text fig. 1.)

The runner habit

The plumule (stem apex) in the cotyledonary sheath does not form any bud scales which might by their elongation produce the dropper; but the walls of the cotyledonary sheath elongate after the primary root is established, and develop the dropper with the plumule as the terminal bud therein. This appears to be constant for all the species of the genus. In the subsequent stages in the several western species, and in *E. albidum* and *E. mesochoreum*, the main stem apex is thrust out as the runner bud within the elongated sheath formed by the clasping petiole. This is exactly comparable to the dropper of the seedling, in that the bud is carried forward passively and contributes nothing to the development of the structure. In the case of the second runner of *E. albidum* and of each of the three runners in *E. americanum*, the runner is formed by the bud itself forming the runner sheath by the elongation of its outer scale. The development of this type of runner introduces a new structure into the series present in the life cycle of the other species, and the degree to which this

innovation is developed may be taken as an index to the divergence from the original type. On this basis the most divergent species is *E. americanum*, with *E. albidum* and *E. mesochoreum* in order toward the type. *Erythronium propullans* is a special case, in which the bud axillary to the foliage leaf (text fig. 3, bud *2*) in immature plants (as of *E. americanum*) is functional in the mature individuals, being elevated above the base of the bulb by the growth at the base of the aerial shoot, as this raises the base of the leaves to their final position. In floral characters it is most nearly related to *E. albidum*. The reduced size of the flower is probably

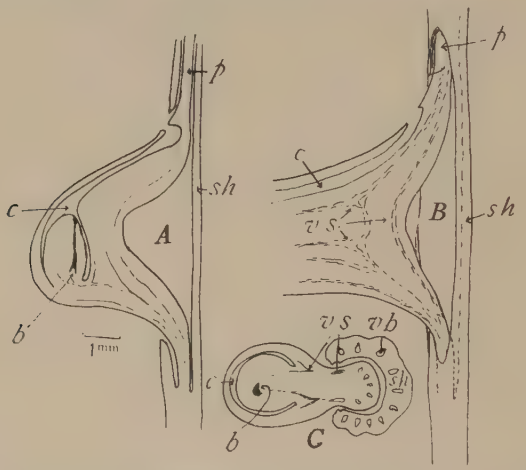

FIG. 5.—Offshoot of *E. propullans*, showing structure and vascular elements in sections: *A*, *C*, on base of older offshoot *B*; *b*, bud of offshoot; *c*, cavity about bud.

due in a measure to the interference with normal nutrition of the flower caused by the diversion of a portion of the vascular supply of the peduncle into the developing runner. The bud from which the lateral runner develops is inserted on the base of the peduncle in such a manner that in the early stages of growth as a runner the base of the peduncle elongates and thickens. As the clasping petioles (*sh*, text fig. 5) hold the upper part of the peduncle from freely moving upward, the result of elongation is to form an elbow, with the bud at the convex side of the bend. At this stage all the vascular bundles are diverted with the general distortion of the base of the peduncle (*A*). As the runner pushes forward from the

elbow of the peduncle, certain of the peduncle bundles produce branches which grow with the advance of the bud and maintain connection with the main vascular supply of the plant (*B*); but in so doing the total supply available to the peduncle is divided between the runner and the peduncle itself, and the reduced size of the flower appears to be the result.

In the species east of Colorado the aerial portions of the plant disintegrate with the ripening of the seeds, the fruit being prostrate when the seeds are ripe. The species of the Rocky Mountain region and westward do not become prostrate, but as the fruits ripen the stalk becomes a stiff and elastic wand, from the top of which the seeds are shaken. In these the capsule is revolute only at the apex, in the others the capsule splits completely to the base; among the first species the seeds are thrown out of the capsule by shaking; in the second group they are released by the rolling back of the inclosing walls of the prostrate capsule. The Eurasian species *E. Dens-canis* belongs to the second group in respect to its seed dispersal.

The western species differ from the forms of the eastern states in details of bulb development. In the eastern forms the region of fusion between the bulb tissues and those of the bud is small; and the sheath inclosing the bud, either in the case of the runner bulbs or when renewed *in situ*, is free from the developing bulb for most of its surface; but in the western forms the elongated bulb has a long fusion zone along the axial side, where the base of the sheath and the surface of the inclosed bud scale are fused. This appears as a ridge, from the edges of which the husk, in fully formed bulbs, extends around the rest of the bud. The bulbs are as a rule much more attenuate in the western forms than in the eastern, both in the young and in the adult stages. In immature bulbs the tip of the new bulb is often not at all lower than the base of the preceding bulb; this is due to the elongation upward on the part of the bud scales at a rate equal to that of the descent of the base of the new bulb in the petiole sheath. In the older bulbs the descent is decreased, but the elongation of the bulb scales upward from their bases produces the long bulbs characteristic of the group. In the bulbs examined, the species

from the western states have thinner husks than those of the eastern states, except *E. Hartwegii*, which has a tough and thick one like that of *Tulipa*. This form grows in an adobe soil, subject to high temperatures and considerable pressure when the soil dries, which may have its influence in the development of the heavier husk (WARMING 22). The Eurasian species (*E. Dens-canis*) has a very delicate husk, which becomes fragmentary during the development of the new bulb, so that the bulb is but slightly protected. The development of the bulb in this species is similar to that of the western forms, but the zone of fusion on the axial side of the bulb rudiment is more nearly the full height of the bulb scale than in these, extending almost to the tip of the scales, and the stem scar seems to be at the apex of the scale. As a result, the scales are fused together along their adaxial surfaces and the axillary buds are inserted much farther from the base of the bulb than is the case in any other species. The base of the petiole becomes charged with starch, and indistinguishable in appearance or function from a bulb scale. This explains the absence of a husk, formed in the other species from the drying of the sheathing petiolar sheath. The seedling of this species is similar to that of the rest of the genus, but there seems to be less of deepening growth in the immature stages than in any of the species of the United States. It is probable that the period of blooming is attained even more slowly by *E. Dens-canis* than in the other species, if the same relation of depth and flower production is maintained. In some of the western species grown in the Botanical Garden of Johns Hopkins University, it was noticed that they bloomed when the bulbs were much smaller in proportion to the average mature size than do those of the eastern forms. It may be that the same early blooming is present both in the Eurasian and in the western species, and that the bulbs continue to descend gradually during a long period after the blossoming habit is inaugurated. Such a point is physiological rather than morphological, and will not be discussed further at this time.

In the runners of *E. americanum* occasional "stimulation growths" have been noticed, apparently related to sudden excess of water. These are due to the bud inclosed by the runner bursting

through the tip of the runner, just as the runners burst the petiole sheath when first issuing from the bulb. The next scale of the bulb rudiment forms the runner extension, and the stem apex with a small scale is carried forward as if under normal conditions. The necessary nourishment for the added growth comes from the parent plant, through the stalk of the runner to the point where the terminal bud was inserted. Then the vascular bundles of the bud, following down through the bud scale, convey material to the stem apex in the tip of the extension of the runner. In two cases, in the spring of 1908, this extension of the runner by the protrusion of the terminal bud through the end of the runner sheath had been repeated a second time.

Development of the mature plants

The production of the flowers, which mark the maturity of the individual plant and the termination of the cycle of stages from seed to seed (text fig. 6), is associated with several changes from the manner of development followed during the immature condition. During the whole period from seedling to this stage, the primary stem apex has persisted, and from it have come the successive leaf rudiments which developed into either bulb scales or foliage leaves as the conditions demanded. The accompanying tabular view of the activity of the primary stem apex will show the general relation of these leaf rudiments. In addition to the outgrowths from the apical dome in the form of leaf rudiments, there have been various buds, axillary to the inner scale, which were laid down by the stem apex from time to time. The leaf rudiments developed in these axillary buds are not considered in the tabulated series of products from the stem apex. The bud in the axil of the outer scale does not arise from the apical tissue directly, but from the mass of meristem at the base of the scales.

The final structure developed from the primary stem apex, after passing through the immature stages, is the flower bud of the mature individual. In the immature stages the apical dome persists at the base of the bulb, producing successively the several bulb scales and foliage leaves. In the mature bulb the apical dome becomes surrounded by the foliage leaf rudiments (fig. 25),

and the whole structure becomes elevated above its original position by the elongation of the tissue below the insertion of the leaves. In the production of the flower bud, at the summit of the aerial shoot, the original stem apex comes to an end. The renewal bud for the next bulb is formed as a bud in the axil of the inner bulb scale, at the base of the shoot (figs. 25*b*, 26, 27).

GENERAL SEQUENCE OF FOLIAR OUTGROWTHS FROM THE STEM APEX IN ERYTHRONIUM AMERICANUM

Vegetative period	Foliar structures				Bulb sequences
	Sequence	Character	Function	Fate	
First	First leaf	Cotyledon	Photosynthesis	Withers	
	Second leaf	First scale	Dropper	Husk	Primary bulb
	Third leaf	Second scale	Storage	Bulb scale	
Second	Fourth leaf	First green leaf	Photosynthesis	Withers (husk?)	
	Fifth leaf	Third scale	Storage	Outer scale	Second bulb
	Sixth leaf	Fourth scale	Storage	Inner scale	
Third	Seventh leaf	Second green leaf	Photosynthesis	Withers*	
	Eighth leaf	Fifth scale	Runner	Husk	Third bulb
	Ninth leaf	Sixth scale	Storage	Bulb scale	
Fourth	Tenth leaf	Third green leaf	Photosynthesis	Withers*	
	Eleventh leaf	Seventh scale	Runner	Husk	Fourth bulb
	Twelfth leaf	Eighth scale	Storage	Bulb scale	
Fifth	Thirteenth leaf	Fourth green leaf	Photosynthesis	Withers*	
	Fourteenth leaf	Ninth scale	Storage	Outer scale	Fifth bulb
	Fifteenth leaf	Tenth scale	Storage	Inner scale	
	Sixteenth leaf	Fifth green leaf (and flower stalk)†	Photosynthesis	Withers	

* If the bulb is renewed *in situ*, the base of the leaf becomes the husk of the new bulb; if the new bulb develops as a runner bulb, the runner sheath forms the husk.

† With the development of the floral axis the activity of the primary stem apex ceases, a branch apex forming the renewal bulb thereafter.

This bud is evidently the homologue of bud *2*, of the immature stages, as indicated in text fig. 3. The bud is at first distinctly in the axil of the scale, but with the upward growth of the adjacent shoot it is lifted from its position to one on the base of the shoot itself (figs. 27 and 29, *3*).

The apical dome of this bud develops bulb scales during the

summer and develops into the full-sized bulb during the active period of the aerial shoot at the base of which it lies. Starch for storage is derived both from the photosynthesis of the leaves and from the deposits in the old bulb within which the new bulb

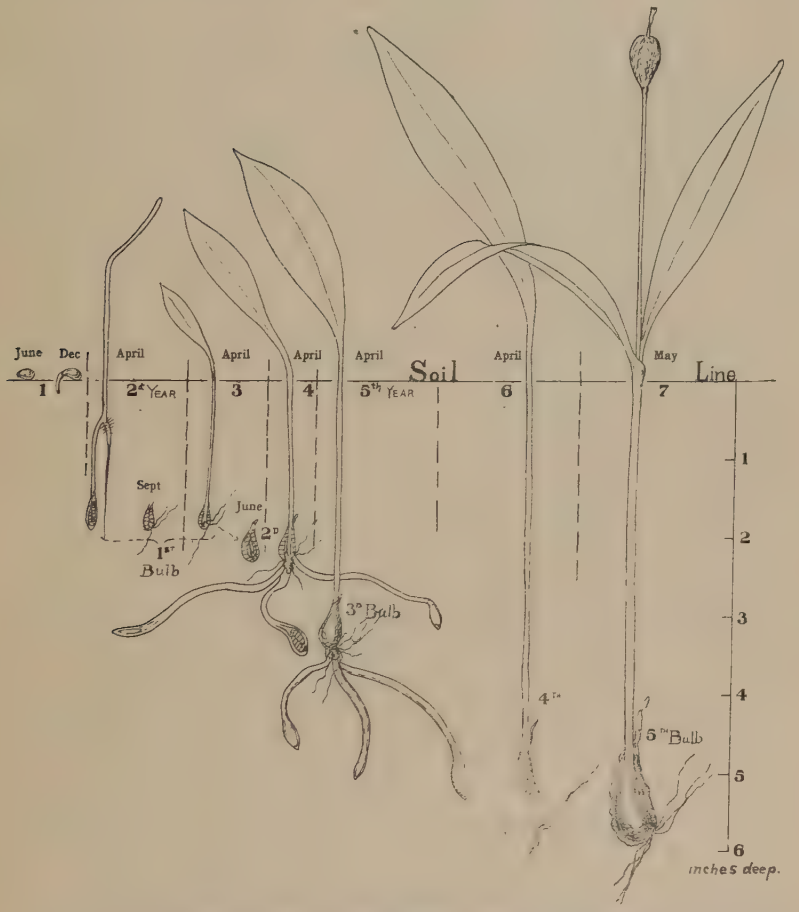

FIG. 6.—Stages in life cycle of *E. americanum:* under natural conditions the third bulb may repeat itself indefinitely, gaining little in depth, being renewed *in situ* for one or more seasons.

is formed. By the time the aerial shoot is dead, the new bulb is mature, and the apical dome within it lays down the rudiments of the next flower. This process is repeated indefinitely, the

individual becoming more robust with time, but otherwise remaining the same. A very slight increase in depth occurs as time passes, since the new bulbs are a little larger than their predecessors, and the new bulb is formed below the center of the old one which it replaces. But a bulb once flowering may revert to the sterile condition after a series of years. Bulbs which have been dug from the soil and allowed to become somewhat dried out are apt to "break," that is, to produce two or three small bulbs instead of the single large one customary in the flowering plants. Bulbs so produced are sterile for at least two years, as found by experiment. This is especially apt to occur if the bulbs are dug while the shoot is actively growing upward through the soil in the spring. Removal of the soil close to a bulb of a flowering plant often causes such to revert to the immature condition and produce runners, even though the flowering of the current season is not hindered by the changed soil conditions.

Individual plants of any age may force the bulb rudiments into abnormal development under the stimulation of unfavorable conditions. A large number of bulbs of various sizes were dug soon after the leaves had pushed through the soil. These with a little soil were left in a tin box for several days; the box was well wrapped and left in a cool room in the meanwhile. Upon inspection ten days later, the leaves were found to have shriveled away, but the bulbs had formed a small bulb from each of the buds which under normal conditions would have developed runners. The starch present in the old bulb and in the leaf furnished the material for the new bulbs, aside from water, which was in the moist soil. This was repeated several times, the exact details varying with the exact condition of the bulbs when dug from the soil. Thus if the runner is already pushing through the base of the bulb, or is further developed, it continues to elongate for several days, but in the end will form the terminal bud into the bulb; it apparently transfers to it the substance of the old bulb and runner stalk as if under normal conditions.

In the descriptions of the liliaceous ovary, the placentae are usually said to come from the incurved margins of the carpellary leaves. In *Erythronium*, however, the margins of the carpels

appear to come into blunt contact, but do not curve inward. The margins unite along the line of contact, and the partitions are formed from a median rib projecting inward from each carpel (figs. 34, 35), meeting at the center of the ovary (TEMPLE 21). In the full-grown ovary, as at fertilization, the evidence for this interpretation of the case is found in the double bundles along the line of dehiscence in the walls of the ovary, and in the presence of a layer of cells rich in protoplasm which passes around the end of the abutting partitions as they come into contact at the center of the ovary (text fig. 7). The densely protoplasmic cells which line the ovary along the line of the placentae continue around the end of each median wing, as shown in the photograph. This series of surfaces of slight contact determines the dehiscence of the ripe capsule.

FIG. 7.—Transverse section of fertilized ovary of *E. americanum*, showing abutting placentae (*p*), two-celled embryo (*e*), and double bundle at edges of fused carpels (*b*); ×25.

Occasional plants are found with sterile anthers on one or more of the stamens, some patches showing many of the plants with no functional pollen. It has been found that the sterility of the anthers begins at least as early as the divisions of the pollen mother cells, as buds have been examined in which three of the anthers were normal, and had normal pollen grains; while the sporogenous tissue of the others was degenerating (fig. 35, *m*, *m'*); the other tissues of the anthers were normal in appearance. In the field it has been noticed that the plants with dark pollen on the stigma had the larger fruits and the larger number of seeds. Plants having pale anthers often lacked pollen entirely, and their seed-developing power seemed to be deficient also. The plants of the two types, fertile with dark stamens and poor with pale anthers, each occur in patches often of considerable numbers. This may

account for the poor set of seed in such cases, for insects working over the patch would not bring in so much viable pollen to the weak plants as if there was a commingling of the two.

Development of seeds

The fertilized ovule enlarges rapidly, mainly through the growth of the embryo sac. The sac destroys the nucellus except a crushed remnant at the bottom of the sac. The raphe and chalazal spur enlarge at the same time, and add to the bulk of the seed as a whole. The endosperm develops slowly, remaining for a considerable time as a layer lining the wall of the sac between the base and the suspensor at the tip. The embryo first develops a considerable mass of cells in the micropylar end of the sac, from the inner free surface of which the functional embryogenic cells are developed (COULTER 7). This inner surface may become lobed, and then gives the condition called polyembryony by JEFFREY (13) and SCHAFFNER (20). Twin embryos developed in one case out of several hundred seeds germinated in this work; these were united near the upper end, but completely free below, and their vascular systems were distinct. These embryos probably were formed from two adjacent lobes from the free surface of the suspensor, becoming united through the incorporation of some cells in common from the base of the lobes. In pushing into the soil, the elongation had occurred in the zone just behind the stem apex, and this was distinct in each of the two embryos, producing the condition shown (fig. 36).

The general conditions of the sac, endosperm, and suspensor in *E. americanum* are closely duplicated in *Urtica cannabina*, as studied by MODILEWSKY (15). In both cases there is a thin lining of free endosperm nuclei along the walls of the sac, a considerable suspensor at the tip, and a mass of deeply staining cells below the base of the sac. In *Erythronium* these cells form a considerable mass, and extend backward to the termination of the raphal bundle at the chalaza. These cells stain deeply even in ripe seeds, and the adjacent cells of the remnant of the nucellus remain in close contact with the center of the base of the endosperm in the ripe seed. This would indicate the purpose of these cells

to be that of transfer agents for substances from the chalaza to the embryo sac, and thence to the forming embryo and endosperm.

When the seed reaches its full development the embryo sac is filled with hard endosperm of reserve cellulose. The cells in the endosperm have their longer axes directed inward from the periphery, curving somewhat toward the micropylar end of the seed. Through the center of the endosperm there is sometimes the same cellular endosperm as elsewhere, more frequently this is nearly solid cellulose. Immediately about the embryo there is usually a small mass of less firm endosperm, which in some cases extends to the surface of the seed, filling the space earlier occupied by the suspensor. It is probable that germination is aided materially in such cases, as moisture can more promptly reach the embryo by this path than would be the case if only thick-walled endosperm were present. At the base of the seed the endosperm shows considerable shrinking, with the remnant of the nucellus remaining in contact with the endosperm for a small area near the center. This secures contact between the hard endosperm and the spongy spur, and even when the spur has disappeared the inner layers of the tissue at the chalaza remain in intimate contact with the base of the endosperm. As the endosperm along the axis of the embryo sac is the last to be deposited, it is probable that the mass of spongy cells in contact with the base is of advantage in the imbibition of water preliminary to germination. In different seeds the exact appearance of the central portion of the endosperm varies from nearly solid, with infrequent cell cavities, to a condition similar to that of the peripheral endosperm; the latter is less common than is the solid core mass. The exact distribution of the cell cavities in the endosperm is probably in close relation to the moisture conditions during the late stages of ripening of the seed. In germination the embryo first enlarges to occupy the space filled by the spongy endosperm in which it lies; then the cotyledon, acting as a haustorial organ, dissolves a path for itself along the axis of the endosperm. The solvent action extends along the lines of cell cavities toward the periphery, and the endosperm is absorbed almost completely.

Completion of the cycle

The individual which began with the germination of the seed and the organization of the stem apex in the sheath at the base of the cotyledon, has been followed through the series of changes normal to its development as *Erythronium americanum*, and the variations have been indicated between this species and the others of the genus. The cycle of the sporophytic generation is thus completed, and the original stem apex culminates in the formation of the flower parts of the first blossom produced by the bulb on reaching maturity. It was shown that the species were structurally related with a large group, the western species, behaving similarly, the others diverging more or less from the habits of these forms. The structures involved in the divergence from type are those most active in the immature stages, and most freely produced in *E. americanum*. This species, therefore, has been regarded here as the most remote from the ancestral form, since the majority of the species are of the more simple type of development in the vegetative habits. The species having the uniform vegetative habits are native to the region from the Rocky Mountains westward, becoming more abundant in species as the Pacific coast is approached, and culminating in a series of habitats in southwestern Oregon. This may be assumed to be near the original home of the genus, from which the distribution and differentiation into the present habitats and species have occurred. It is probable that the lines of migration have followed the present lines of specific distribution, especially in the United States. The single species of Eurasia combines the bulb characters of the western species with the withering aerial parts of the eastern forms. The character of the habitats in which this species occurs may be so nearly uniform that no marked variations have been developed from the original type, beyond that involved in the prostrate fruit. Ants have been observed carrying the seeds of *E. americanum*, and it is probable that they aid in distribution in each of the species having seeds with fleshy raphe or spur tissue. This would include *E. Dens-canis* as one of the myrmechochorous species, as a considerable chalazal spur is present, comparable to that of *Viola* or *Sanguinaria* (Beal 1), but not so large as that of *E. americanum* or *E. albidum*.

Summary

The points presented in this paper may be summarized as follows:

The undifferentiated embryo begins to elongate in the fall and organizes a rudimentary stem apex in a narrow cavity at the base of the cotyledon. In germination the radicle is thrust into the soil during the winter, the stem apex following immediately behind the base of the radicle, in the cavity mentioned. The hypocotyl is represented by the fusion region between the vascular supply to the stem apex and the main vascular system of the seedling; it takes no part in the development of the seedling. After absorbing the endosperm, the cotyledon is elevated into the air, and acts as the first photosynthetic organ. Either two or three vascular bundles are present, varying with the species.

During the activity of the cotyledon as a leaf, the cavity in the base of the cotyledon about the stem apex elongates to form a slender sheath, with the stem apex inclosed as a terminal bud at the tip. The "dropper" so formed is positively geotropic in response, as is the primary root; the runners and roots of later stages are not positively geotropic. At the close of the season the terminal bud of the dropper is isolated in the soil by the withering of other parts of the plant.

During the summer the first foliage leaf is organized by the stem apex and becomes functional the following spring. Roots are protruded at the base of the bulb in the fall, which marks the beginning of the second vegetative period. This sequence of development is repeated in the subsequent seasons to the mature bulbs.

The stem apex becomes inclosed by the base of the foliage leaf, and there forms a bud from which the next bulb will develop. When the bulb is renewed *in situ*, only this bud develops; this is also the rule in the species producing but one runner. In *E. americanum* two buds are usually formed in addition to the main bud, each of which elongates as a runner and forms a bulb. These additional runners spring from buds axillary to the leaf, or to a bulb scale. When but one runner is developed normally by a species, it is formed from the elongation of the base of the petiole, which carries the bulb rudiment into the soil as a terminal bud,

as in *Tulipa*. The additional runners when present, and all three in *E. americanum*, are developed from the elongation of the outer scale of the bud, the inner scale and the apical dome forming the terminal bud of such a runner.

The vascular connection between the stem apex and the point of insertion of the runner is to be considered cauline, the rest of the runner tissue as foliar and apical. The structure of the runner in *E. americanum* is that of an anatropous bud, the outer surface of its external scale being fused with the upper surface of the supporting stem; the latter maintains vascular connection between the base and the apex of the structure developed. The zone of growth of the fusion structure is located as in normal rhizomes, close to the tip of the structure; both the scale and the cauline tissue take part in the elongation.

The mature plants form the floral shoot from the stem apex, the new bulb being developed from a bud, at the base of the shoot. The stem apex of the new bud forms the next flower, and the bulb is renewed in turn from a bud axillary to the inner scale of the bulb rudiment. The bud in the axil of the outer scale usually dies without developing.

Using the runner habit as the basis of comparison, the genus is divided into two groups, one occurring typically at low elevation, and producing two or three slender runners from short bulbs, the other at higher elevation and forming but one runner and developing into slender bulbs. A form intermediate between the two occurs in western Kansas and Nebraska. An aberrant form occurs in a restricted locality in Minnesota, having a lateral runner developed from a bud in the axil of a foliage leaf.

The interval between germination and flowering on the part of an individual is at least six years. This minimum is liable to indefinite increase under average conditions, by the interpolation of additional immature bulbs because of the formation of the runner bulbs no deeper than the parent bulb, or by the suppression of runners in a particular year.

The distribution of the species points to the Pacific coast as the probable home of the genus, the present distribution being the result of migration along lines connecting the habitats of the

present forms. The species are found to vary from the type found in the assumed original habitat approximately in proportion to the distance of migration. The species of Eurasia combines features of the two groups in its vegetative characters.

The roots radiate from a point near the base of the bulb, but show no definite response to gravity; they maintain a definite space relation to each other, defining the surface of a cone in the soil, the axis of which is about 45° to the vertical. In development, the roots arise in September from cells just below the vascular base of the bulb, and grow in straight lines during their elongation. In penetrating the bulb tissue, the cells are apparently dissolved by the root tissue, making a cavity about the advancing root rudiments. The number of roots increases with the age of the bulb.

Conclusions

From the foregoing study the following conclusions may be drawn: The delayed development of the embryo is associated with a large store of endosperm; this is drawn upon by the germinating embryo during the season when vegetative activity is low; the young seedling is established in the soil early in the spring, the endosperm furnishing the needed materials for its development. With the exhaustion of the reserve material of the seed, the primary root is developed, and the cotyledon is elevated into the air and light; the cotyledon is the only leaf exposed to the light by the seedling. The stem apex, located in a narrow cavity in the base of the cotyledon, is carried forward by the elongation of the embryo, and, after the elevation of the cotyledon, is carried farther into the soil by the elongation of the walls of the cavity. The short period of vegetative activity, and the prompt descent of the stem apex in the dropper, would indicate adjustment to short growing seasons; the brevity of the active season is a feature of the life cycle. The tendency on the part of the seedling to bury the stem apex deeply is continued by the immature plants in the production of runners; in some cases these are strictly comparable to the dropper of the seedling in structure, in others they involve new developments; but the result is the same in either case.

The persistence of the original stem apex until the establish-

ment of the flower axis allows for the repetition of an indefinite series of immature bulbs, formed from runners or *in situ*, but introducing no new structures during the whole period of immature development. With the formation of the flowering shoot, the vegetative structures become secondary in importance, and the renewal bulb is developed from an axillary bud at the base of the shoot. The continuation of the individual is thereafter without vegetative multiplication normally, the increase being secured by the seeds.

The geographical distribution of species and their relation to each other in structural details indicate that the genus originated in that region of the Pacific coast now included in the state of Oregon, and has been distributed along lines approximately following the present habitats of the several species. In the progress of migration the advancing species developed special methods for rapid descent into the soil, which in some forms has become a means of numerical increase.

In the development of means of vegetative multiplication, elongation of the structure immediately about the stem apex (in the seedling the base of the cotyledon, in the western forms the base of the petiole) was followed by the elongation of the scales of axillary buds, thus forming additional descending axes, each of which developed an additional bulb from its terminal bud. One species has developed a runner from a bud axillary to the foliage leaf, apparently being derived from the adjacent form in which the second runner arises from a bud axillary to the inner scale. The production of this lateral runner is confined to the flowering plants, since only in these is the leaf axil elevated above the base of the bulb. This form is very restricted, and appears to be the species most recently derived from the parent stock, or from some other species as these are now known.

The general development in the genus would confirm the assumption that it is related to *Tulipa*, especially through *T. sylvestris*.

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EXPLANATION OF PLATES VIII–X

PLATE VIII

All figures drawn on the same scale, which is indicated by the measured line; drawings made by means of a vertical projecting lantern from the stained sections.

FIG. 1.—Dormant embryo in endosperm; *i*, remnant of inner integument.

FIG. 2.—Embryo about December 1, still within seed; *s*, position of stem apex; *e*, endosperm.

FIG. 3.—Descending tip of seedling; stem apex in slit at *a*.

FIG. 3*a*.—Cross-section of seedling at line *a–b* of fig. 3.

FIG. 4.—Tip of cotyledon in longitudinal section, showing haustorial cells (*h*) and vascular cells (*v*).

FIG. 5.—Cross-section of cotyledon; *v*, vascular bundles; *s*, stomata.

FIGS. 6–13.—Stages in the development of the dropper about the stem apex (*s*).

FIGS. 11, 12.—Two sections of the same dropper, showing scale leaf (*l*) and stem apex (*s*); *t*, plumule trace.

FIG. 13.—Stem apex as terminal bud in tip of active dropper, as in April.

PLATE IX

Magnification the same as in plate VIII, except in figs. 21, 22, 23, 25, in which the magnification is indicated.

FIG. 14.—Stem apex in late June at bottom of bulb.

FIG. 15.—Stem apex (*s*) and rudiment of foliage leaf (*l*) in July.

FIGS. 16–20.—Cross-sections of young dropper, from base of cotyledon downward, showing hypocotyl region (17), separation of root and dropper (18), and dome of stem apex (20).

FIGS. 21, 22.—Cross-sections of active and dead root steles; *e*, endodermis; ×250.

FIG. 23.—Active runner marked to show zone of maximum elongation after three weeks' growth; natural size.

FIG. 24.—Base of bulb, showing sheathing petiole (*p*), stem apex (*s*), and root rudiment (*r*), as found August 1.

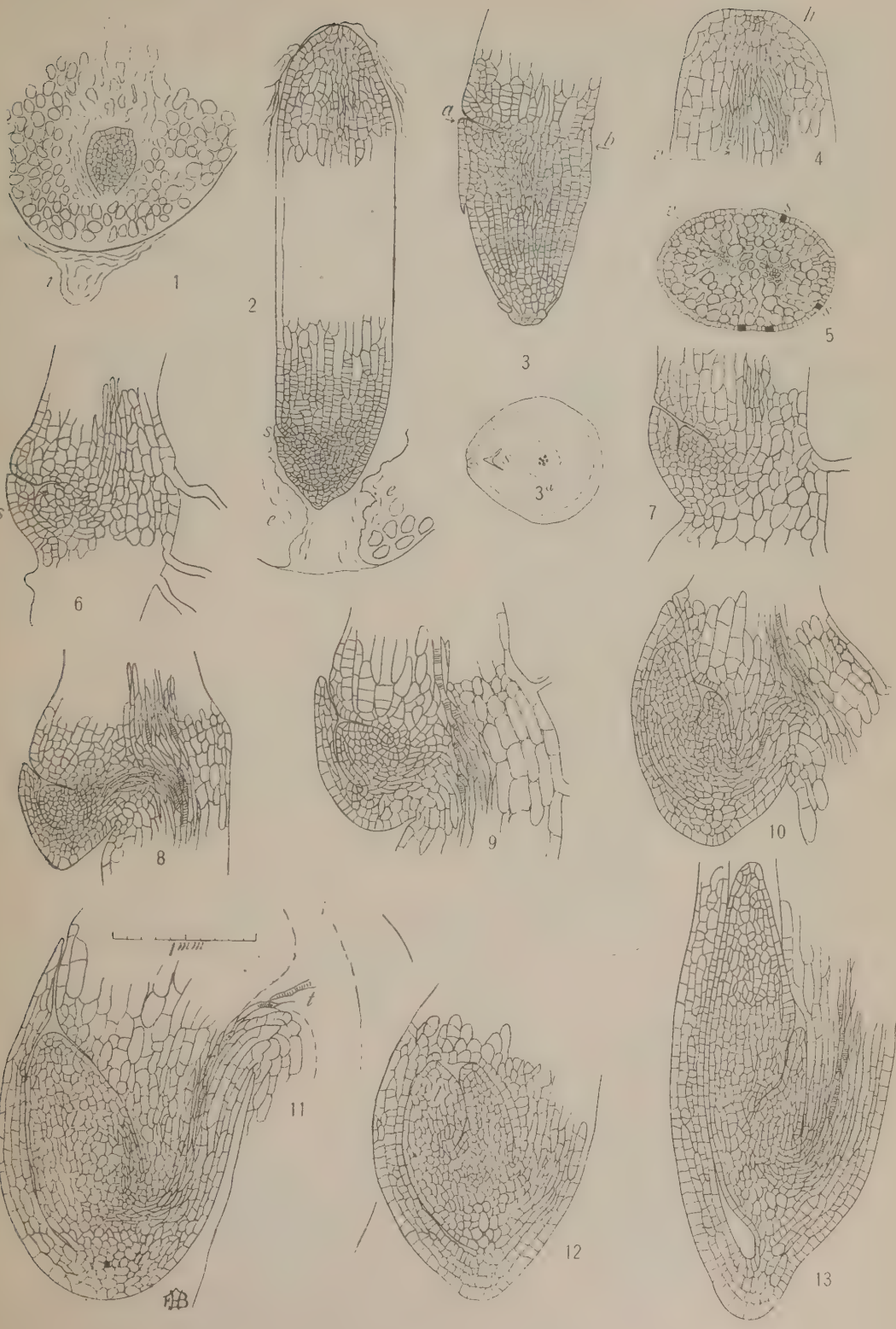
FIG. 25.—Outline of stem apex in flowering bulb, showing flower rudiment (*f*) inclosed by the foliage leaves (*l*) and the location of the renewal bud (*b*); ×10.

FIG. 26.—Renewal bud from the same section showing apical dome above and root rudiment below the scale; July 1.

FIG. 27.—The same structures about August 1, on the same scale.

PLATE X

Figs. 28, 28*a*, 34, 35 on a uniform scale, the same as in previous figures; figs. 29–33, 36 as indicated.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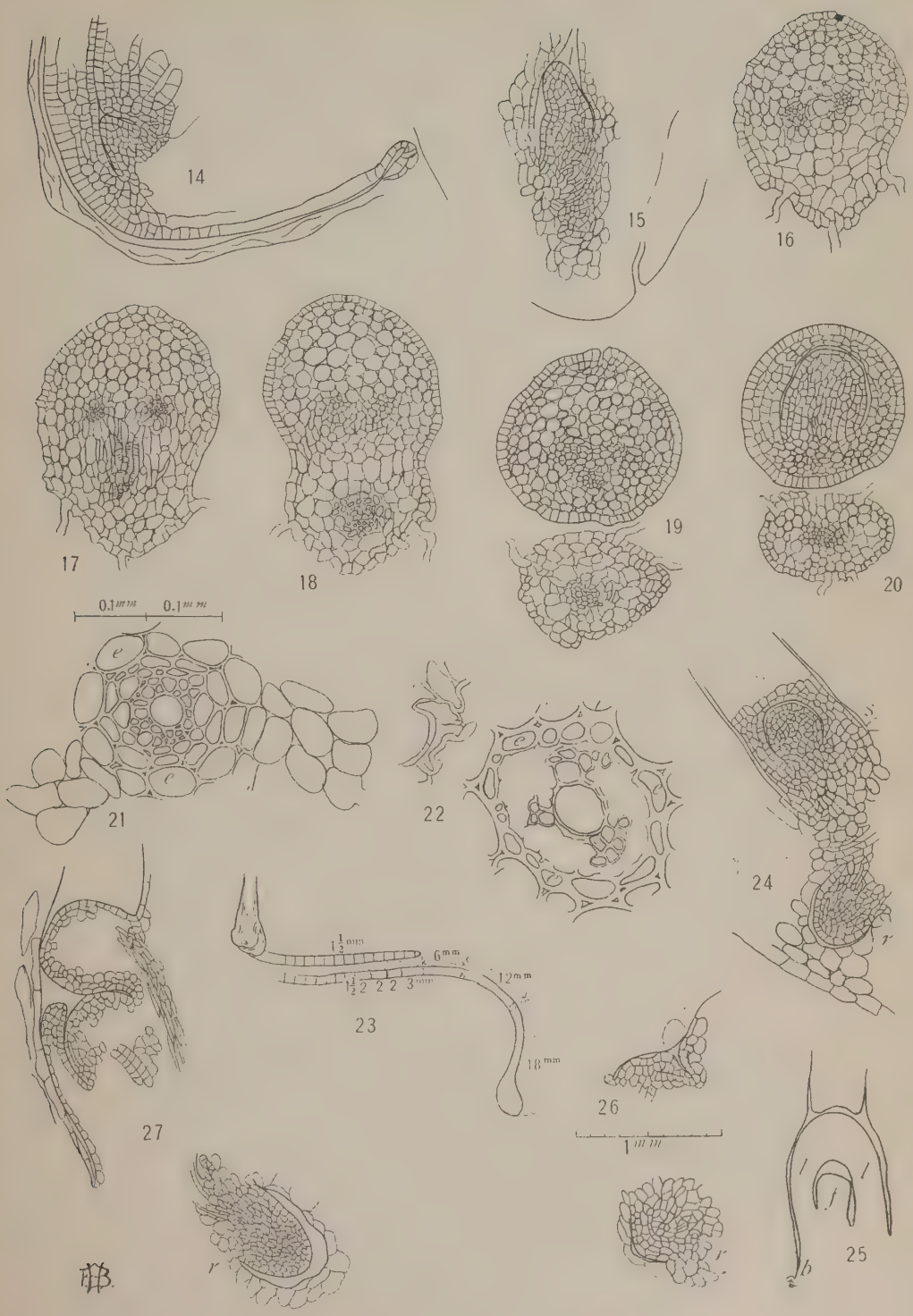
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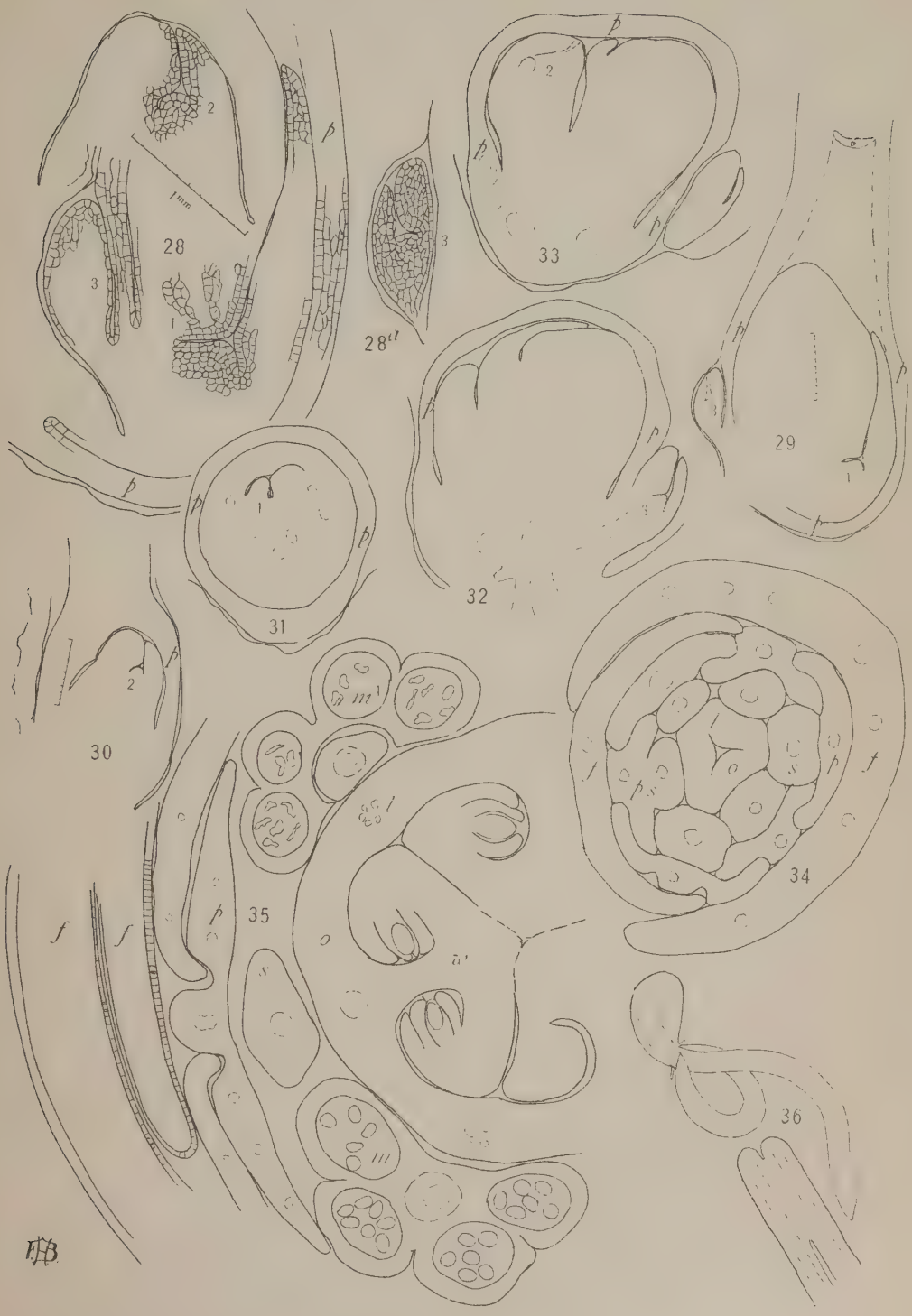
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FIG. 28.—The three buds in the immature bulbs of *E. americanum; 1*, main stem apex; *2*, bud axillary to leaf; *3*, bud axillary to scale; *1* and *3* on the same section.

FIG. 28*a*.—Sagittal section of bud *3*, to show apical dome.

FIG. 29.—Outline of entire section shown in fig. 28; relation of buds *1* and *3*.

FIG. 30.—Similar section in reference to bud *2;* in each the sheathing base of the petiole is *p*.

FIGS. 31–33.—Cross-sections of bulb rudiment, showing relation of the same structures as shown in figs. 28–30; the sections follow in order of their numbers but are not consecutive.

FIGS. 34, 35.—Cross-sections of developing flower bud in early September and early December, on the same scale and in the same orientation; *f*, foliage leaves; *p*, petals; *s*, stamens; *o*, ovary wall; *l*, line of dehiscence (lateral margin of carpel); *w*, wing-placenta from median region of carpel; *m*, *m'*, normal and degenerating microspores.

FIG. 36.—Twin embryos of *E. americanum*, ×5; the union of the two cotyledons shown below in outline.

BIOGRAPHICAL NOTE

Frederick H. Blodgett was born in Rockford, Illinois, September, 12, 1872. He received the degree of B.S. in 1907 and the degree of M.S. in 1909, from Rutgers College. For two years he filled positions in experiment station and botanical museum work, and in 1901 went as assistant plant pathologist to the Maryland Agricultural College. Since 1906 he has been in residence at Johns Hopkins University, having resigned from the Agricultural College at the end of the year 1906–7. In the summers of 1906, 1907, 1908, he was engaged with Dr. Forrest Shreve in field work and writing on a Report upon the Plant Life of Maryland, now in press as Volume III, *Maryland Weather Service;* and in the academic years of 1906–7, 1907–8, 1908–9, and 1909–10 was assistant in botany in this University.